Drought and grazing: IV. Blue grama and western wheatgrass

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Abstract

An understanding of the impacts of grazing during and following drought on rangeland ecosystems is critical for developing effective drought management strategies. This study was designed to examine the effects of drought and grazing on blue grama [Bouteloua gracilis (H.B.K) Lag. ex Griffiths] and western wheatgrass [Pascopyrum smithii Rydb. (Love)] tiller growth dynamics. Research was conducted from 1993 to 1996 at the Fort Keogh Livestock and Range Research Laboratory located near Miles City, Mont. An automated rainout shelter was used during 1994 to impose a severe late spring to early fall (May to October) drought on 6 of twelve, 5- x 10-m non-weighing lysimeters. Twice replicated grazing treatments were: 1) grazed both the year of (1994) and the year after (1995) drought; 2) grazed the year of and rested the year after drought; and 3) no grazing either year. Drought had minimal impact on tiller relative growth rates of plants grazed twice, although it reduced ($P \le 0.01$) rates of axillary tiller emergence for blue grama (79%) and western wheatgrass (91%). Defoliation periodically increased relative growth rates (P \leq 0.05) and tiller emergence (P \leq 0.01) of both species. Neither drought nor grazing affected tiller densities or tiller replacement rates of either species nor did they affect productivity of blue grama. Drought, however, reduced ($P \le 0.01$) productivity of western wheatgrass 50% in 1994 whereas grazing reduced productivity (P ≤ 0.01) by 46% in 1994 and 69% in 1995. Moderate stocking levels (40-50% utilization) during and after drought did not adversely affect the sustainability of these dominant native grasses.

Key Words: Bouteloua gracilis, Pascopyrum smithii, production, rainout shelter, rest, water potential

The Northern Great Plains support 7 million animal units (AUs) in the U.S. and Canada (USDA 1993, Willms and Jefferson 1993). Campbell (1936) stated that 2 or 3 years out of 10 would be drought years in the Northern Great Plains. Drought and grazing can affect plant productivity and decrease plant longevity (Ludlow 1986). Large portions of plant communities within the Northern Great Plains are dominated by blue grama (*Bouteloua gracilis*,

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Resumen

Un entendimiento de los impactos del apacentamiento durante y después de la sequía en los ecosistemas de pastizal es critico para desarrollar estrategias efectivas de manejo de la sequía. Este estudio se diseño para examinar los efectos de la sequía y el apacentamiento en al dinámica de crecimiento de los hijuelos de "Blue grama" [Bouteloua gracilis (H.B.K) Lag. ex Griffiths] y "Western wheatgrass" [Pascopyrum smithii Rydb. (Love)]. La investigación se condujo de 1993 a 1996 en el Laboratorio de Investigación de Ganado y Pastizales Fort Keogh cerca de Miles City, Mont. Durante 1994 se utilizo un protector de lluvia automatizado para aplicar una sequía severa de fines de primavera e inicios de otoño (Mayo a Octubre) en 6 de los 12 lisímetros de 5 x 10 m. Los tratamiento de apacentamiento se repitieron 2 veces y fueron:1) apacentado en el año de la sequía (1994) y el año signiente (1995), 2) apacentado el año de la sequía y descansado el año siguiente y 3) sin apacentamiento en ambos años. La sequía tuvo un impacto mínimo en las tasas relativas de crecimiento de los hijuelos de plantas apacentadas doble, aunque redujo (P \le \text{ 0.01) las tasas de emergencia de hijuelos auxiliares del "Blue grama" (79%) y "Western wheatgrass" (91%). La defoliación periódica incremento las tasas relativas de crecimiento ($P \le 0.05$) y la emergencia de hijuelos (P < 0.01) de ambas especies. Ni la sequía ni el apacentamiento afectaron las densidades de hijuelos o las tasas de remplazo de estos en ninguna de las especies, tampoco afectaron la productividad del "Blue grama". Sin embargo, la sequía redujo la productividad (P \le 0.01) de "Western wheatgrass", en 50% en 1994, mientras que el apacentamiento redujo la productividad ($P \le 0.01$) en 46% en 1994 y 69% en 1995. Niveles moderados de carga (40-50% de utilización) durante y después de la sequía no afectan adversamente la sustentabilidad de estos zacates nativos dominantes.

[H.B.K] Lag. ex Griffiths) and western wheatgrass (*Pascopyrum smithii*, Rydb.). It is apparent that these 2 plant species have evolved with the combined effects of drought and herbivory. Therefore, it is important when managing rangelands to know how individual plants persist in the face of these stressors.

Many researchers have examined the role of tillers in plant survival (Richards et al. 1987, Olson and Richards 1988, Bullock et al. 1994, Zhang and Romo 1995), but quantitative studies on the impacts of grazing during and after drought on tiller population dynamics are lacking. It has been hypothesized that grazing during and following drought can suppress recovery rates of individual plants as well as plant communities (Pieper and Heitschmidt

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1988, Burkhardt 1996). To test this hypothesis, we examined the effects of grazing during and after a growing season drought on xylem water potentials, tiller relative growth rates (RGR), seasonal axillary tiller emergence, annual tiller replacement, tiller densities, and aboveground net primary production (ANPP) of blue grama and western wheatgrass. Heitschmidt et al. (1999) have published effects of drought on soil water, vegetative productivity and plant species composition.

Materials and Methods

Study Area

This study was part of a large rainout shelter project conducted on the USDA, ARS Fort Keogh Livestock and Range Research Laboratory near Miles City, Mont. (46°19'45'N 105°49'45'W). This area is representative of the semi-arid mixed grass prairie of the Northern Great Plains. Native vegetation on the 22,500-ha research station is a grama-needlegrasswheatgrass (Bouteloua-Stipa-Agropyron) mix (Küchler 1964). Long-term annual precipitation averages 34-cm (NOAA 1996) with about 60-70% received during the mid-April through mid-September growing season (Fig 1). Temperatures may exceed 38°C during summer and decrease to -40°C during winter. The average frost-free period is 150 days.

The experiment was conducted from 1993 to 1996 on native rangeland that had not been grazed 2 years prior to the study. Precipitation was 30% (530 mm) above average (NOAA 1996) the year before the study. The study site was located on a gently sloping (4%), clayey range site in high fair range condition. The soils were very deep, well-drained, fine, montmorillonitic, frigid Aridic Ustochrepts. Vegetation at the site was dominated by blue grama (40–45% by weight) and western wheat-grass (30–35% by weight).

Lysimeters and Treatments

Twelve, 5- X 10-m non-weighing lysimeters were arranged perpendicularly to the slope along a 65-m transect in 2 groups of 6 lysimeters with a 5-m area between groups within a grazing exclosure. An automated rainout shelter was constructed to control the amount of precipitation received on 1 of the 2 sets of 6 lysimeters. The 12- X 35-m metal framed "roof" was mounted on 15-cm diameter plastic wheels atop seven, 5-cm wide rails stationed about 75-cm above the soil surface. Rails extended from the top edge

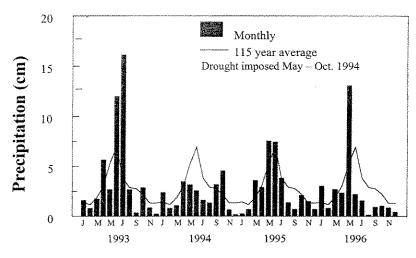


Fig. 1. Monthly precipitation (cm) from January 1993 through December 1996 and long-term (115 yr) average at Miles City, Mont. including the drought treatment in 1994 (NOAA 1996; Heitschmidt et al. 1999).

(i.e., upslope) to 15-m below the bottom edge of the lysimeters. Rails were located directly over lysimeter borders. The shelter was equipped with a moisture sensitive conductance plate that when wetted, activated a small electric motor and its associated drive system, which moved the shelter across the lysimeters.

Following the 1993 pre-treatment baseline year, twice replicated treatments were: 1) grazed during the year of drought and rested the year after, hereafter referred to as G94; 2) grazed both the year of the simulated drought and the year after, hereafter referred to as the G94-95; and 3) rested in all years, hereafter referred to as the ungrazed treatment (UG). The same 3 treatments were repeated in the nondrought set of lysimeters. Lysimeters were grazed intensively with 6 ewes and their twin lambs for a few hours in early June and early July of both 1994 and 1995 to achieve 40-50% utilization. The simulated drought was imposed (1 growing season) from mid-May to early October 1994.

Precipitation, Soil Water, and Xylem Water Potentials

Precipitation was monitored on site using standard rain gauges (Heitschmidt et al. 1999). Soil water was estimated a minimum of once a month from April through October at depths of 15-, 30-, 60-, 90- and 120-cm using a dielectric soil water probe (Heitschmidt et al. 1999).

Xylem water potentials of blue grama and western wheatgrass plants growing in the ungrazed drought and non-drought treatments were estimated on 7 dates between 18 May and 28 July, 1994 and 6 dates between 15 May and 2 August, 1995. Measurements were made at 0430 and 1230 hours on the youngest fully expanded leaves of individual plants using standard pressure chamber techniques (Scholander et al. 1965). Sample plants were randomly selected along a transect within each lysimeter. Sample size per species/sample date/sample time/lysimeter was 1 in 1994 and 2 in 1995.

Tiller and Production Measurements

Six permanent 14- X 18-cm quadrats per lysimeter were randomly established within mixed blue grama and western wheatgrass communities. Quadrat locations were restricted to areas not previously sampled, and at least 50-cm inside the plot edge. Colored wire rings were used to permanently identify 10 study tillers per quadrat, 5 each of blue grama and western wheatgrass. The same quadrats were used for the duration of the research. If a marked tiller produced axillary tillers at anytime during the growing season, the axillary tillers were marked with a different color to distinguish them from primary tillers. Different tillers were marked in the same manner in 1995.

From an initial population of 360 tillers per species, repeated, season-long measurements (n = 17 in 1994; n = 14 in 1995) were taken on 270 blue grama and 329 western wheatgrass tillers in 1994 and 320 blue grama and 341 western wheatgrass tillers in 1995. Differences between marked and measured tillers were due to lost markers or excluding data from tillers which were not grazed twice. Tiller measurements began in mid-May and continued weekly through August with additional measurements for quantification of any autumn

(1984), since the rainout shelter size and cost precluded classical treatment replication. The use of a single rainout shelter to test the effects of drought is common in the literature (Busso 1988, Busso et al. 1989, 1990, Frank and Rics 1990, McSmith and Ritchie 1992, Busso and Richards 1993, 1995). Statistical tests used in our study were conservative, since the experimental units were not quadrats, individual plants or individual tillers. In addition, analyses were conducted in a manner similar to the first paper in this series similar to the first paper in this series

Results

Precipitation, Soil Water, and Water Stress

In 1993, the pre-treatment year, total annual precipitation was 38% above the long-term average of 34-cm (Fig. 1). Annual precipitation in 1994 was 24.7-cm, 24% below average. Precipitation from 1 May to 31 October 1994 was 16.3 cm compared to the 27.1-cm average. Total annual precipitation for 1995 and 1996 was similar to the long-term average (Heitschmidt et al. 1999);

Heitschmidt et al. (1999) previously reported no differences in soil water dynamics between imposed 1994 drought and natural precipitation and grazing treatment lysimeters. The only significant main effects were year and date.

the imposed drought) as well as 1995. ment plots during 1994 (i.e., the year of in both the drought and non-drought treatthe magnitude of water stress was similar species ($P \ge 0.86$) interactions showed that 0.18) and drought freatment-by-date-bynificant drought treatment-by-date (P \geq ing soil water content. The absence of sigincreasing water potentials with decreastollowed anticipated seasonal trends of of the total sum of squares. The date effect tials. Species accounted for less than 5% predawn and 58% for midday water poten-85% of the total sum of squares for the most important factor accounting for and their interaction (P < 0.01). Date was species (midday; $P \le 0.01$), date ($P \le 0.01$) Water potentials were affected by plant or western wheatgrass (P = 0.40; Table 1). potential of either blue grama (P = 0.93) either pre-dawn or mid-day leaf water The drought treatment did not affect

Utilization

Minety-eight percent of marked blue grama tillers (265 of 270) in 1994, and 97% (309 of 320) in 1995 remained in a

and dates in the model. Years and/or dates and all associated 2- and 3-way interactions were analyzed as within plot repeated measures and tested using full model residuals (Heitschmidt et al. 1999).

Pre-dawn and mid-day water potential data were analyzed separately using repeated measures AOV with drought treatment, plant species, and date as main effects. The error terms for testing the main effects of drought treatment interaction. The error terms for testing the main effects of species and the interaction effects of species and the interaction effects of species and drought treatments were replimated treatment by species. The full model residuals were used to test the repeated measures effects of dates and all associate 2- and 3-way interaction effects. Growth precures entre and all associate 2- and 3-way interaction effects.

Growth records were summarized using average tiller relative growth rate within 3 time periods were: 1) the last 2 weeks of May before the first grazing event; 2) the entire month of June between the first and second grazing event; and 3) July to October of 1994 and July to early September 1995. The number of 1994 post-grazing sampling dates was of 1994 post-grazing sampling dates was both species were essentially dormant throughout both summer periods.

A univariate, repeated measures analysis of variance model was used to analyze filler relative growth rate data. A 2-way AOV was used to determine the effects of drought and grazing on percent tiller recruitment. Tiller relative growth rates and tiller recruitment are reported for tillers that were grazed twice, since the majority (> 85%) of the tillers in the lysimeters were grazed during both grazing events. This was done to reduce confounding effects of combining once grazed and twice grazed tillers.

Tiller densities from May 1994 (i.e., pre-treatment) were included as a covariate in the 2 following years' data. Means were considered to be significantly different when $P \le 0.05$, unless noted otherwise. Individual lysimeters were considered experimental units for all analyses.

Heitschmidt et al. (1999) reported plant functional group and species compositional differences among treatment plots in 1993. We initially used the pre-treatment year (1993) blue grama and western wheatgrass productivity estimates as covariates in subsequent year analyses. Since the covariates were never significant (P \geq 0.22), they were subsequently excluding

Drought treatments might be considered pseudo-replicated, according to Hurlbert

ed from the final analyses.

growth, Information gathered on an individual tiller during each visit included: plant height, phenology, number of leaves, axillary tillering and tiller senescence.

O°C for 48 hours before weighing. sented. All segments were oven dried at plants found in the lysimeters were reprelar to Tusler (1993), so all height ranges of for western wheatgrass in a manner simiments of 1-cm for blue grama and 3-cm were cut from the base upward in segately cut into segments. Tiller bundles transported to the laboratory and immedigrama tillers were placed in plastic bags, ing 5 western wheatgrass and 10 blue grazing event, Individual bundles containthe lysimeters were collected before each range of heights for those tillers found in Five bundles per species representing the other ullers of the same height (+/-1 cm). the soil surface and bundled together with species, tillers were measured, clipped at near vicinity of the lysimeters. For each ed on the same clayey range site in the neight-weight relationships of tillers locatwere converted to biomass by developing mass through time. Height measurements vented direct estimates of cumulative bio-Measuring tillers nondestructively pre-

Tiller relative growth rates (g g ¹ day ¹) were calculated according to Radford (1967) as:

Tiller relative growth rates = (log_e W_{t+1} - log_e W_t) * I^{-1}

where W was filler weight (g), t was initial time, and I was time increment in days.

Density of western wheatgrass was determined by counting total number of live tillers within each quadrat. Because of the "mat-like" growth form of blue grama, density was determined by counting the number of tillers within a 5,75-cm² circular plot, or 2% of the quadrat area, randomly located within each permanent domly located within each permanent quadrat. Densities were measured on 24 domly 1994, 1995, and 1996.

Standing crop inside 20 randomly located 250-cm² quadrats per lysimeter was harvested monthly by species from 1993 to 1996 (Heitschmidt et al. 1999). Samples were oven dried at 60°C, separated into live and dead components and then weighed. Aboveground net primary production was calculated for blue grama and western wheatgrass by summing all positive increases in standing crop from April to November.

Data Summarization and Analyses

Soil water measurements were analyzed using repeated measures analysis of variance (AOV) with year, depth, treatments

Table 1. Predawn and midday leaf water potentials (MPa) for western wheatgrass (Pasm) and blue grama (Bogr) plants growing in drought and nondrought lysimeters at Fort Keogh in 1994 and 1995.

Year		Pre-c	iawn²	Mid-day²		
	Date	Pasm	Bogr	Pasm	Bogr	
	· · · · · · · · · · · · · · · · · · ·	*****		(MPa)		
1994	18 May	-0.32d	-0.42d	-2.36cde	-0.62e	
	31 May ³	-0.24d	-0.31d	-2.81bcd	-2.12cd	
	14 Jun ³	-0.44cd	-0.20d	3.62ab	-2.69bc	
	23 Jun ³	-0.75cd	-1.39c	-3.16abc	-2.11e	
	30 Jun	-4.18a	4.04b	~2.90bcd	-2.29cd	
	13 Jul ⁴	-1.04bc	-4.92a	4.00a	-4.28a	
	28 Jul^3	-4.46a	-5.00a	-3.15abc	-4.48a	
1995	15 May	-0.43cd	-0.26d	-1.58e	-0.71e	
	2 Jun	-0.99bc	0.59d	-2.22de	~2.08cd	
	16 Jun	-0.51cd	-0.31d	-2.48cd	-1.75d	
	$30 \mathrm{Jun}^3$	-0.46cd	-0.50d	-2.02de	-0.70e	
	17 Jul	-1.42b	-1.42c	-2.84bcd	-2.62bcd	
	2 Aug	-3.88a	-4.25b	-3.18abc	-3.30b	

There were no significant (P ≥ 0.10) differences in drought versus nondrought treatments.

vegetative phenological stage. On average, utilization was 39% and 47% on blue grama tillers for the first and second grazing events in 1994, and 23% and 45% for the first and second grazing events in 1995. Over 85% of the marked blue grama tillers in the grazed lysimeters were grazed twice in both years.

Ninety-eight percent (323 of 329) in 1994 and 94% (322 of 341) in 1995 of marked western wheatgrass tillers remained in a vegetative phenological stage during the growing seasons. On average, utilization was 49% and 51% for the first and second grazing events in 1994 and 53% and 46% for the first and second grazing events in 1995. Over 90% of marked western wheatgrass tillers were grazed twice in 1994 and 1995.

Tiller Relative Growth Rates

Analyses of relative growth rates of twice-grazed blue grama tillers revealed significant ($P \le 0.01$) treatment-by-time interactions (Fig. 2). Relative growth rates were reduced (P = 0.01) 29% by drought before grazing treatments were imposed (i.e., May) but not different ($P \ge 0.30$) from June through October in 1994 (Fig. 2). Growth rates of defoliated tillers were 107% greater ($P \le 0.01$) than undefoliated tillers after the first grazing event (i.e., June), but similar (P = 0.08) thereafter and not different ($P \ge 0.10$) from zero from July through October (Fig. 2).

The year following the imposed drought (i.e., 1995), the blue grama time-by-drought (P = 0.02) and time-by-grazing treatment interactions were significant ($P \le 0.01$). In May, relative regrowth rates

were 18% greater (P = 0.01) for plants exposed to the imposed 1994 drought than for non-drought plants, but rates were similar (P \geq 0.30) thereafter (Fig. 2). Relative growth rates in the ungrazed treatment during May 1995 were 19% greater (P = 0.02) than in either grazing treatment. However, following the first grazing event of 1995 (i.e., June), relative growth rates were greater (P = 0.02) in the G94-95 treatment than the ungrazed control and greater (P = 0.003) than the G94 treatment. Relative growth rates from July through August were not different (P \geq 0.10) from zero (Fig. 2).

Relative growth rates of marked western wheatgrass tillers grazed twice, were unaffected by drought in 1994 (P = 0.61). Relative growth rates were greater (P \leq 0.01) in the 2 grazed treatments (G94 and G94-95) compared to the ungrazed treatment (0.007 vs. 0.002 g⁻¹ day⁻¹) in June, and declined from July to October (Fig. 3).

Tiller relative growth rates were not different ($P \ge 0.15$) from zero from July through October (Fig. 3).

Results were similar for western wheat-grass in 1995 in that relative growth rates were unaffected by drought treatment (P = 0.69), were greater ($P \le 0.01$) in the grazed (G94-95) than the 2 ungrazed (G94 and ungrazed) treatments in June, and declined through the season (Fig. 3).

Tiller Recruitment

The percent of primary blue grama tillers which produced an axillary tiller, varied during the 1994 growing season in response to drought and grazing (Table 2). Drought reduced ($P \le 0.01$) total recruitment 80%, whereas grazing increased ($P \le 0.01$) recruitment 315% compared to ungrazed treatments. Sixty percent of daughter tillers were produced after the first grazing event. Of those producing axillary tillers, none in the drought treatment produced more than 1 axillary tiller. Eighteen percent in the non-drought treatment produced 2 secondary tillers.

In 1995, the magnitude of recruitment by blue grama was similar (P = 0.16) between drought and non-drought treatments (Table 2). Tiller recruitment for combined grazing treatments was 78% greater ($P \le 0.01$) than without grazing. Ninety-eight percent of the tiller recruitment occurred after the first grazing event. On average, 30% of the blue grama tillers producing axillary tillers produced 2 secondary tillers. It appeared that the seasonal pattern of axillary tillering by blue grama was similar in 1994 and 1995.

Recruitment by western wheatgrass tillers grazed twice also varied in magnitude between the 1994 drought and grazing treatments (Table 2). Drought reduced $(P \le 0.01)$ recruitment 91% (Table 2). Grazed tillers exhibited greater (P = 0.04)

Table 2. Least square means (%), SE and P-values proportions of marked primary tillers that produced at least I axillary tiller during the growing season for blue grama and western wheat-grass subjected to drought and grazing treatments.

٨	Drought Treatments ¹				Grazing Treatments ²					
Year	D	ND	SE	P	G94	G94-95	UG	SE	P	$D*G^3$
Blue Grama ⁴		- (%)				(%)		**		
1994	8a	40b	3	≤ 0.01	31a	32a	10b	3	≤ 0.01	0.08
1995	39	49	4	0.16	47a	60a	30b	5	0.01	0.50
Western Wheatgrass										
1994	7a	79b	3	≤ 0.01	47a	46a	35b	3	0.04	0.07
1995	6	11	3	0.18	5	15	6	3	0.12	0.84

D = Drought, ND = Non Drought.

Means within columns with different letters are significantly different at P \leq 0.05.

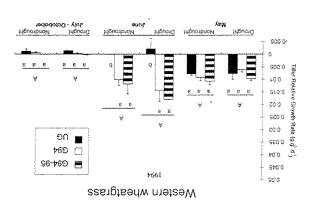
Significant (P \leq 0.05) mid-day species effects.

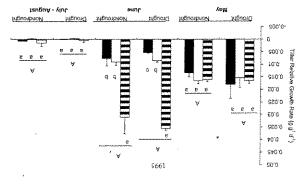
⁴Significant (P ≤ 0.05) predawn species effects.

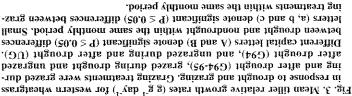
²G94 = Grazed in 1994, G94-95 = Grazed in 1994 and 1995, UG = Ungrazed.

D*G = Drought by grazing interaction P-value.

⁴Drought or grazing treatment means in the same year (row), with different letters are significantly different at P ≤ 0.05.







quorght-by-tiller interactions occurred either in 1995 or 1996. No significant (P ≥ 0.20) Grazing did not (P = 0.49) affect densities drought (9,967 vs. 6,263 tillers m⁻²). greater (P = 0.02) than not subject to stands subjected to drought were 59% imposed, tiller densities of blue grama but in 1996, 2 years after the drought was drought in 1995 (8,068 vs. 9,420 tillers m⁻²), grama were not (P = 0.10) affected by and 1996 analyses. Tiller densities of blue were included as covariates for the 1995 lysimeters in 1994, Initial tiller densities not $(P \ge 0.60)$ among grazing treatment lysimeters (8,646 vs. 9,854 tillers/m²) but 1994 in drought compared to non-drought

(2000) = 0.007) in 1996 (476 vs. 814 tillers m drought in 1995 but were reduced 42% (P densities were not (P = 0.71) affected by Tiller 1995 but not (5.12) in 1996. Tiller their covariates were significant ($P \le 0.04$) wheatgrass were different (P \le 0.01) and Initial (1994) tiller densities of western

> same sufflerences between grazing treatments within the same same monthly period. Small letters (a, b and c) denote significant (P oth middle should be the second and mondrought within the drought (UG). Different capital letters (A and B) denote significant ungrazed after drought (G94), and ungrazed during and after during and after drought (G94-95), grazed during drought and response to drought and grazing. Grazing treatments were grazed Fig. 2. Mean tiller relative growth rates (g g 1 day 1) for blue grama in

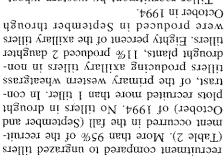
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Blue grama

96-1/60



daughter tiller in 1995. wheatgrass tillers produced more than I (September-October) of 1995. No western grass tillers were recruited in the fall (Table 2). Only 26% of the western wheatgrazing (P = 0.12) treatments in 1995 lar between drought (P = 0.18) and among grass during the growing season was simi-Tiller recruitment by western wheat-

Tiller Density

monthly period.

800.0

90010

10.0 9100 20.0

52350 50.03

92016

0.04

G4010 5010

\$9010

980.0

40,0 200.0 g

90%

99010

of blue grams were greater (P = 0.06) in Estimated pre-treatment tiller densities

.8661 no 2661 ni grazing treatment (P ≥ 0.52) interactions = 0.49) by grazing treatment or drought by

ments. Tiller densities were not affected (P

when compared to non-drought treat-

(11.0 = 9) and another (Feq. (1993)) gramma (i.e., 1993) did not differ (Feq. (1993)) (Table 3). Pre-treatment ANPP for blue har across years and grazing treatments Blue grama production averaged 551 kg (ddNA) Aboveground Net Primary Production

were not significant ($P \ge 0.10$) in any year. Drought-by-grazing treatment interactions effects were non-significant (P ≥ 0.10). showed all drought and grazing treatment Analyses for years 1994 through 1996 ment plots than the ungrazed (Table 3). ereater (P = 0.03) in the 2 grazed treatbetween drought treatments, but it was

greater (P = 0.05) in the G94-95 and between drought treatment plots, but was wheatgrass did not differ (P = 0.10)Estimated 1993 ANPP for western

Table 3. Least square means (kg ha⁻¹), SE, and P-values for aboveground net primary production estimates for blue grama and western wheatgrass subjected to drought and grazing treatments.

Year	Drought Treatments ¹				G			,		
	D	ND	SE	P	G94	G94-95	UG	SE	P	D*G ³
Blue Grama ⁴	(kg	ha ⁻¹)			~ ~ ~ ~ ~ ~	(kg ha ⁻ⁱ)				
1993	1,473	1,276	78	0.11	1,421a	1,588a	1,101b	96	0.03	0.14
1994	712	639	90	0.58	680	566	781	110	0.43	0.10
1995	564	476	81	0.47	562	334	663	99	0.13	0.48
1996	516	398	64	0.24	395	357	619	78	0.10	0.90
Western Wheatgrass4										
1993	1.117	1.687	211	0.10	1,138a	1,595b	1,472b	259	0.05	0.49
1994	649a	1.277b	90	≤ 0.01	757a	756a	1,378Ь	110	10.0	0.98
1995	978	1,376	129	0.07	1,608a	481b	1,442a	158	≤0.01	0.17
1996	961	1.347	166	0.15	1.275	1,029	1,157	204	0.70	0.40

D = Drought, ND = Non Drought.

ungrazed treatment plots than the G94 treatment plots (Table 3). Pre-treatment ANPP were not significant ($P \ge 0.22$) covariates in any initial analyses, therefore, they were not included in the final analysis. Aboveground net primary production was less (P = 0.01) in the drought than non-drought treatment in 1994 and greater (P = 0.01) in the ungrazed than grazed treatments (G94-95) in 1994. The only difference found thereafter, was that ANPP in G94-95 (which was grazed in 1995) was less (P \leq 0.01) in 1995 than in the 2 nongrazed treatments in 1995 (NG and G94). There were no drought by grazing treatment interactions ($P \ge 0.17$) in any year.

Discussion

Based on the results of this study, we conclude that: 1) relative growth rates of tillers which were grazed twice, were largely unaffected by drought and seasonally enhanced by grazing (Fig. 2 and 3); 2) axillary tillering was impeded by drought during the growing season and enhanced by grazing (Table 2); 3) tiller densities were unaffected by drought or grazing; and 4) neither drought nor grazing affected blue grama ANPP whereas drought reduced western wheatgrass ANPP with mixed grazing treatment effects (Table 3).

The major effects of drought were expressed by a slight (19%) reduction in tiller relative growth rates of blue grama in May 1994, a large reduction in tillering for western wheatgrass (91%) and blue grama (80%) during the growing season in 1994, and a large reduction of ANPP for western wheatgrass. Growth and tillering are often reduced by water stress (Brown 1995). Zhang and Romo (1995) reported the number of emerging northern wheatgrass

(Agropyron dasystachyum (Hook.) Scriton.) tillers was positively correlated with soil water. Haferkamp et al. (1997 and 1998), Haferkamp and Heitschmidt (1999) and Rummell (1946) reported western wheatgrass tiller density increased with the removal of competition of Japanese brome (Bromus japonicus Thunb.).

The responses to the initiation of the drought began to appear early in 1994 as shown by the change in blue grama tiller relative growth rates and the lack of a significant date-by-treatment interaction for western wheatgrass tiller relative growth rates. However, the response to the imposed drought and control lysimeters were similar due to the natural droughtlike conditions which existed during 1994. Precipitation was 24% below average, and this drought caused plants to be equally water stressed by May 1994 regardless of drought treatment (Table 1). This conclusion is also supported by the precipitation (Fig. 1), xylem water potentials, and soil water data reported previously by Heitschmidt et al. (1999).

Our results also suggest the effects of a 1-year drought on growth rates did not carry over to the next year. Carry over effects may have been limited by the initial drought as well as above average precipitation that fell in March, April, and May 1995. Busso and Richards (1995) and Busso et al. (1989) did not find the effects of a 1-year drought on numbers of active axillary buds carried over to the next year. Only after 3 consecutive years of drought did Busso et al. (1989) find reduced numbers of metabolically active axillary buds.

Fewer axillary tillers were produced by western wheatgrass in 1995 than in 1994. Increased western wheatgrass tillering is associated with increased fall precipitation the previous year (Haferkamp et al. 1997). However, in this instance, the fall of 1994

was wetter than fall of 1993 (Fig. 1). Thus, the reduction of tillering in 1995 was more likely due to the dry summer of 1994.

Grazing had little long-term effect on blue grama or western wheatgrass. The increase in tiller recruitment with grazing during the growing season agrees with findings of Sims et al. (1973). They reported mowing blue grama plants in late June and early July stimulated additional tillering, mostly from reproductive shoots that had elevated above the mowed height. Mowing earlier in the growing season depressed tillering, whereas mowing in late July and early August stimulated tillering, but insufficient growing season remained for complete development of these late tillers. They also reported increased tillering with mowing for sand bluestem (Andropogon hallii Hack.) a rhizomatous warm-season grass.

Our findings that grazing did not reduce ANPP of blue grama, but did decrease ANPP of western wheatgrass can best be explained by the different morphologies of the 2 species. Grass species like blue grama are characterized by short growing shoots and when grazed, these species can maintain much higher proportions of photosynthetic tissue than can species with long shoots like western wheatgrass (Dahl and Hyder 1977). Klipple and Costello (1960) noted that herbage production of western wheatgrass remained the same when utilization of that species increased from about 10% to about 20% but declined sharply when utilization increased to 40%. Launchbaugh (1967) found that forage production of western wheatgrass declined as utilization increased from 44 to 80%. Reed and Peterson (1961), Everson (1966), and Branson (1953) concluded that forage production of western wheatgrass declined with increased utilization.

²G94 = Grazed in 1994, G94-95 = Grazed in 1994 and 1995, UG = Ungrazed.

³D*G = Drought by grazing interaction P-value.

⁴Drought or grazing treatment means in the same year (rows), with different letters are significantly different at $P \le 0.05$.

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> due to slightly different methodologies. (1999), but our findings were probably tion as reported by Heitschmidt et al. increase in warm-season herbage producimposed drought. We failed to detect an been due to the timing and severity of the change in species composition may have (Heitschmidt et al. 1999). This lack of in this study were not observed 1978). Shifts in plant species composition cipitation is above average (White et al. sition shifts toward mid grasses when pre-(Smoliak et al. 1972), but species compospecies composition toward short grasses al. 1975). Extended drought usually shifts 1958, Reed and Peterson 1961, Hyder et tion of mixed-grass rangelands (Coupland tance of environmental factors on produc-Many studies have shown the impor-

Management Implications

within the conditions of this study. these Northern Great Plains rangelands tainability of dominant native grasses on after drought did not adversely affect suslevels (40-50% utilization) during and western wheatgrass. Moderate stocking tions on the tiller level for blue grama and not be necessary to maintain plant populaafter a 1-year growing season drought may Elimination of livestock grazing during or appear to adversely affect tiller processes. (both during and after drought) did not ing season drought combined with grazing Our results demonstrate a 1-year grow-

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